

Current knowledge on biology, fishing and conservation of the blue shark (*Prionace glauca*)

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Abstract

The blue shark (*Prionace glauca*) is a large predator in marine ecosystems, figuring as the most common and abundant species in oceanic fisheries. For this reason, many studies on this species were conducted throughout its entire distribution range. However, no comparison has been made regarding the variability of the aspects addressed herein. Thus, the present study aims at analyzing the available information on *P. glauca*. This species constitutes between 85 and 90% of the total elasmobranchs caught by oceanic fisheries with pelagic longlines. Growth parameters reveal that individuals in the Atlantic Ocean show the highest asymptotic lengths when compared to those found in other oceans. Females present an average uterine fecundity of 30 embryos. Although it shows a diverse diet, it is mainly composed of teleost fish and cephalopods. Currently, the main threat to the species is commercial fishing, being listed in Brazil and worldwide, according to IUCN as Near Threatened. Regardless, information on crucial aspects, such as its population dynamics, are still scarce or unreliable for many areas. Despite the number of studies regarding its distribution, abundance, and biology, data for new stock assessments of *P. glauca* are still needed to improve the species' management.

Keywords

Conservation, elasmobranch, feeding ecology, growth, reproduction, stock assessment

Introduction

The blue shark (*Prionace glauca* Linnaeus, 1758) is among the most exploited shark species in the world (Coelho et al. 2012), being frequently caught in pelagic longline fisheries (Carvalho et al. 2010), and is the main component of the international shark fin trade (Stevens et al. 2010). Fisheries estimates on the global catch of *P. glauca* for the fin trade suggest that volumes are close to, or possibly exceeding, the maximum sustainable yield (Clarke et al. 2006). Thus, there is an increasing concern regarding the impacts of fisheries on blue shark conservation (Montealegre-Quijano and Vooren 2010).

Considering its representativeness in commercial fisheries and the amount of data available, the objective of the present study was to conduct a review on the existing knowledge about *P. glauca*. These include the species biology, population structure, fisheries statistics, and conservation status. Furthermore, we compare the existing information across oceans and identify recent advances in the knowledge gaps about this species. We conducted a literature search in the ISI Web of Science and Google Scholar using the keywords: “*Prionace glauca*” OR “Blue shark” OR “Tubarão azul”. In a subsequent filtering process, the title, year of publication, locality, authorship, and other information related to the themes present in this study were extracted from the selected articles. Overall, 314 articles were found, of which 27% were included.

Taxonomy and distribution

The blue shark is the only species of its genus, which is included in the Carcharhinidae family (Compagno 1984; Ebert et al. 2013). It is easily recognized, due to its morphological characteristics, such as an elongated body with long pectoral fins, large eyes with a nictitating membrane below the eye, a dark blue dorsal side and white coloration on its ventral side (Nakano and Seki 2003; Nakano and Stevens 2008).

P. glauca is an abundant species, with a wide distribution in all temperate and tropical oceans (Megalofonou et al. 2005; Ebert et al. 2013). The blue shark's distribution is influenced by seasonal variations in water temperature, reproductive cycle, and availability of food resources (Kohler et al. 2002; Werry et al. 2014). Recently, its distribution range was determined to be between 62°N and 54°S (Coelho et al. 2017), expanding the previous distribution (60°N, and 50°S) (Last and Stevens 2009; Mejuto et al. 2014). It can also occur at depths of 152 m (Lessa et al. 2004), reaching up to 1000 m (Stevens et al. 2010).

Fisheries

According to the estimates of global landings of the United Nations Food and Agriculture Organization (FAO), blue shark catches have grown between the 1950s and 2014, with the highest value recorded in 2013, followed by a decrease in recent years (FAO Fishstat Database Plus 2017) (Fig. 1A). Carvalho et al. (2010), correlates

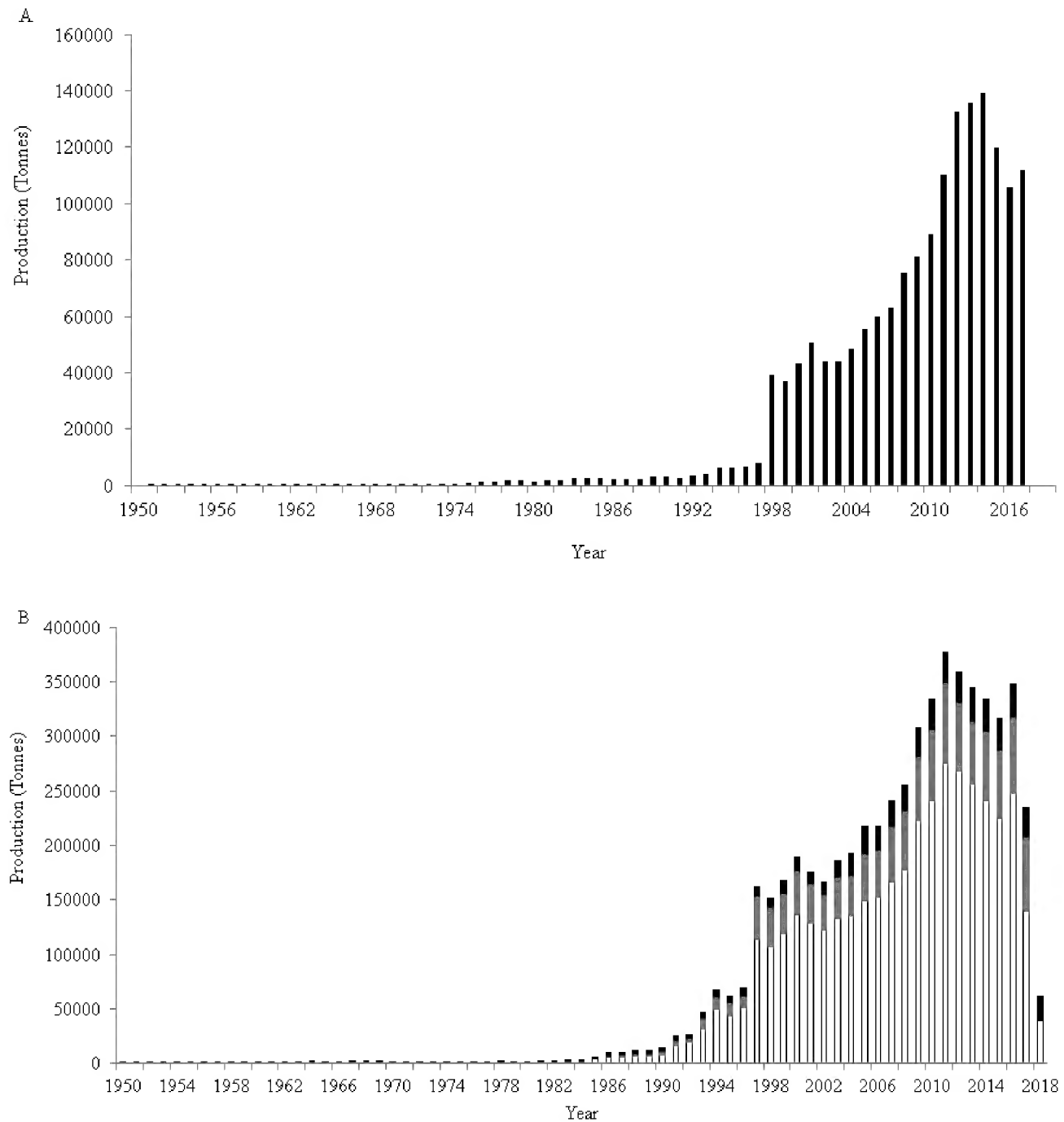


Figure 1. World total production of *Prionace glauca* according FAO (a) and by Ocean (b) (Pacific – White bars, Atlantic – Grey bars and Indic – Black bars).

such growth to the introduction of monofilament in pelagic longlines between 1995 and 1996 targeting swordfish (*Xiphias gladius*), followed by an increase in the meat and fin trades. Based on ICCAT (2015) records, blue shark stocks seem to be slightly overexploited, which may be the reason for the decreases observed. However, these statistics depend on the ability and availability to accurately report fishing data (Bornatowski et al. 2018). Therefore, there is great concern about the limited availability of data due to undeclared and illegal catches (Aires-da-Silva and Galucci 2007). In addition, global discards are mentioned by some authors as a serious problem caused by the lack of accurate estimates, which compromise attempts to provide reliable data on stocks (Bonfil 1994; James et al. 2015), especially for species that can be easily discarded, such as the blue shark. Despite some studies evaluating post-release mortality (discards), the results demonstrate that both combinations of capture and post-release mortalities can far exceed reported landings. Therefore,

the actual mortality may be even higher (Molina and Cooke 2012; Campana et al. 2015; James et al. 2015).

Between the 1980s and 2000s, the blue shark was commonly captured as bycatch in fisheries targeting tunas (*Thunnus* spp.) and swordfish (*X. gladius*) (Coelho et al. 2003; Carvalho et al. 2010; Mourato et al. 2011). However, with the increase in trade, the species became increasingly targeted by commercial oceanic fisheries. Although many developing countries have a high consumption of shark products and byproducts (i. e. meat, fillets, nutritional supplements, and fin soup) (Clarke 2004; Lee et al. 2015), some regions, such as Brazil, consider shark meat to be of low quality. Hence, they are sold under generic names, such as “cacao” (common name attributed to any shark or rays), for better consumer acceptance, in addition to being sold without labeling and with lower prices (Bornatowski et al. 2018). The species also became the focus of recreational fishing (Clarke 2004; Campana et al. 2006; Clarke et al. 2006; Fordham 2006; Aires-da-Silva and Gallucci 2007), which consists of a shark catch tournament in which animals are released after capture. Blue sharks make up more than 90% of recreational fishing landings (Campana et al. 2006).

As the species with the highest rate of capture in the Atlantic, Pacific and Indian oceans, *P. glauca* has been the subject of discussion by international and regional fisheries management organizations (RFMO's), such as Western and Central Pacific Fisheries Commission (WCPFC), Indian Ocean Tuna Commission (IOTC) and International Commission for the Conservation of Atlantic Tunas (ICCAT) (Tsai et al. 2015). Among the three oceans in which it is distributed, the Pacific Ocean exhibits the highest volume of reported catches (Fig. 1B). In general, five species of sharks including the blue shark stand out in catches in the Pacific Ocean, with an average of 2 million individuals caught annually (Clarke et al. 2013) since the mid-90s (Lawson 2011). According to the records of the WCPFC, a commission that aims to assess and manage impacts on bycatch species associated with tuna, blue shark catches grew gradually, with a peak in 2011 (Fig. 1B). However, there are reports of declines in catch rates, of about 5–7% per year between 1995 and 2010 in the Pacific Ocean (Clarke et al. 2013) followed by an increased trend (Tsai et al. 2015). A similar pattern has been observed in the Indian Ocean, where reported catch has grown since the early 1990s (Clarke et al. 2013).

In the Atlantic, average landings registered by ICCAT from 2010–2014 were approximately 64,000 tons, 58% from the North and 42% from the South Atlantic (Coelho et al. 2017). According to Coelho et al. (2012), *P. glauca* represents about 50% of the total catch volume considering all fish and about 90% considering only elasmobranchs. However, reported levels of capture in the Atlantic may not represent what is actually caught, as most sharks are discarded at sea (finning), without being recorded both onboard and in landing sheets (Campana et al. 2005; Aires-da-Silva and Gallucci 2007). Recently, the evaluation method carried out by ICCAT expressed concern about the fact that some series of CPUEs used are doubtful (Carvalho et al. 2010). For this reason, it is suggested that the blue shark is being exploited at rates close to or above a maximum of sustainable production (Clarke 2004).

Biology

Age and growth

There is a vast amount of age and growth studies for *P. glauca* worldwide (Table 1). In these, age and growth parameters are estimated using length-frequency distribution analyses (Megalofonou et al. 2009), as well as readings of age annuli in vertebrae and X-rays (Stevens 1975; Cailliet et al. 1983; Manning and Francis 2005; Blanco-Parra et al. 2008; Jolly et al. 2013; Joung et al. 2017).

Estimates of growth parameters according to the von Bertalanffy (1938) model for combined or separate sexes (L_{∞} and k), vary substantially between studies. The oldest study for *P. glauca* (Aasen 1966) suggests an $L_{\infty} = 394$ cm, as well as a relatively low growth rate ($k = 0.133 \text{ y}^{-1}$). However, recent studies show a much lower L_{∞} . Values of k were estimated, varying between 0.10 and 0.22 y^{-1} , while L_{∞} varied between 243.3 and 402 cm. The variability between age and growth estimates might be a result of the size difference of sampled individuals, which may result in a non-representative length range, thus leading to biased parameters (Cailliet and Tanaka 1990). Individuals from the Atlantic Ocean had the highest asymptotic lengths when compared to those from other oceans but the growth coefficient did not present large variations (Fig. 2AB). The Indian Ocean has only one study on age and growth.

In the North Atlantic Ocean, the average size of *P. glauca* was significantly higher when compared to Pacific and Indian oceans. Stevens (1975) observed that the blue shark grows up to an asymptotic length of 300 cm TL in 10 years, and the age annuli are formed in the spring. In a study performed by Skomal and Natanson (2003) also in the North Atlantic, the maximum length found was 312 cm for the age of 16 years, and the validation data indicated that annuli were formed in the spring, thus corroborating Stevens (1975). Blanco-Parra et al. (2008) also reported a maximum age of 16 years, similar to studies conducted in both North and South Atlantic oceans.

In the South Atlantic Ocean, Lessa et al. (2004) concluded that *P. glauca* shows a growth band formation between November and January in Brazil, a similar result to the one found by Joung et al. (2017) for this region, where bands formed between May and November. According to Lessa et al. (2004), the age at first maturity is 5 years for both sexes, with a maximum length of 310 cm TL attained at 12 years old. However, Jolly et al. (2013) reported individuals with ages of up to 16 years in the South Atlantic. Joung et al. (2017) suggested that the blue sharks in the Eastern South Atlantic have a lower growth rate than those found in the Western South and North Atlantic.

Reproduction

All studies on the reproductive biology of *P. glauca* report a sex ratio was of one male for each female, except for Varghese et al. (2017), which presented a rate of

Table 1. von Bertalanffy growth parameters for the blue shark, *Prionace glauca*, in the North and South Pacific and North and South Atlantic Oceans. t_{max} is the maximum observed age; and t_{mat} is the observed age at first sexual maturity.

Source	Sex	Length range (cm)	t_0 (years)	L_∞ (cm)	k	n	Length measurement	t_{max} (years)	t_{mat} (years)
<i>Pacific Ocean</i>									
Blanco-Parra et al. (2008)	Combined	81–270	−2.680	303.4	0.100	204	TL	16	–
Manning and Francis (2005)	Male	40–300	−1.257	342.9	0.088	140	FL	22	8
	Female	50–250	−1.047	267.5	0.126	288	FL	20	7–9
Nakano (1994)*	Male	–	−0.756	289.7	0.129	148	PCL	10	–
	Female	–	−0.849	243.3	0.144	123	PCL	10	–
Tanaka (1984)*	Male	–	−0.993	308.2	0.094	43	PCL	–	–
	Female	–	−1.306	256.1	0.116	43	PCL	–	–
Cailliet et al. (1983)	Combined	95–204	−0.802	265.5	0.223	130	TL	20	6–7
<i>Atlantic Ocean</i>									
Joung et al. (2017)	Combined	100–325	−1.310	352.1	0.130	742	TL	15	–
Jolly et al. (2013)	Combined	72–313	−1.660	311.6	0.120	197	TL	16	–
Megalofonou et al. (2009)	Combined	81–315	−0.620	402.0	0.130	54	TL	12	–
Lessa et al. (2004)	Combined	173–310	−1.010	352.0	0.160	236	TL	12	–
Skomal and Natanson (2003)	Combined	49–312	−1.430	286.8	0.170	411	FL	16	5
Henderson et al. (2001)	Combined	64–219	−1.330	376.5	0.120	30	TL	12	–
Aires-da-Silva (1996)	Combined	–	−1.075	340.0	0.138	308	TL	–	–
Stevens (1975)	Combined	42–272	−1.035	423.0	0.110	82	TL	6	–
Aasen (1966)	Combined	–	−0.801	394.0	0.133	268	TL	8	–
<i>Indian Ocean</i>									
Andrade et al. (2019)	Combined	82–301	–	278.3	0.140	679	FL	25	–

5.5 males for each female. The blue shark is a placental viviparous species, with a 9 to 12-month gestation and an average fecundity of 30 neonates per breeding cycle. Size at birth is estimated between 35 and 51 cm (Table 2). Data on fecundity is only available for the Atlantic and Pacific Oceans (Fig. 3). Highest fecundities are reported for the Pacific Ocean, with a sexual proportion for embryos of one male for each female.

Studies on the sexual maturity of *P. glauca* over the years indicate that the average total length between oceans does not vary significantly for males (212 cm) or females (208 cm). However, the highest total lengths for both sexes are reported for the Atlantic Ocean (Fig. 4). This scenario contradicts Pratt (1979), the oldest study performed in the North Atlantic, which suggests that the males reach sexual maturity at an average length of 180 cm, whereas females are divided into three groups: immature (46 to 145 cm); sub-adults (145 to 185 cm), and mature (185 to > 300 cm).

In the North-eastern South Atlantic Ocean, females reach sexual maturity at around 228 cm TL (Hazin and Lessa 2005), while males reach it at 225 cm (5–6 years) (Hazin et al. 1994; Hazin et al. 2000). In the Southwestern Atlantic, maturity was estimated to be at 171.2 cm fork length (FL) for females, and 180.2 cm FL for males (Montealegre-Quijano et al. 2014). Mating occurs in Southern Brazil during the summer, with animals heading towards Northeast Brazil, where ovulation and fertilization occur (Carvalho et al. 2011). In the Southwestern Equatorial Atlantic Ocean, Hazin et al. (1994) observed the predominance of pre-ovulatory

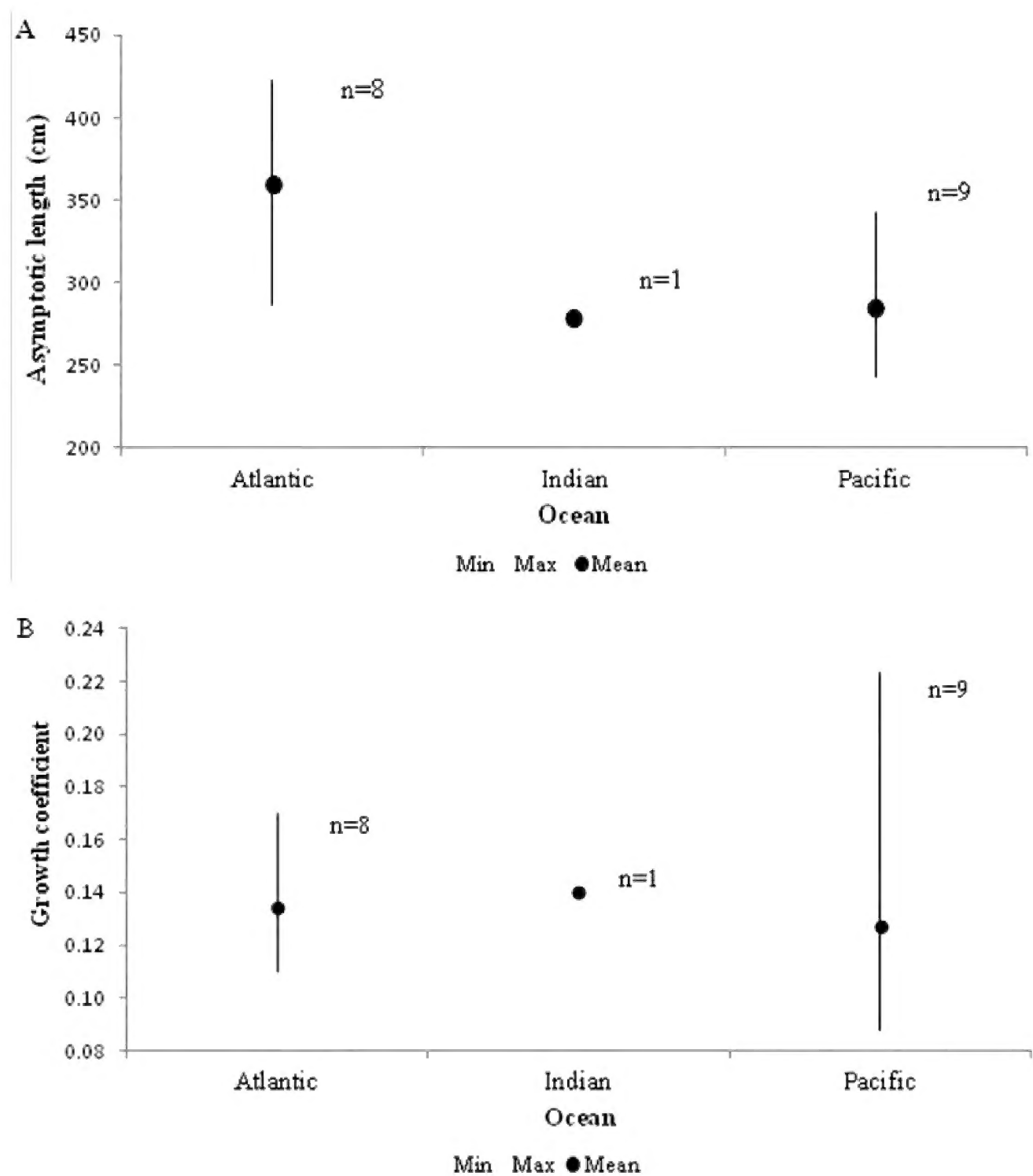


Figure 2. A and B average (dots), minimum and maximum (bars) of the asymptotic length (L_{∞}) and growth coefficient (k).

females in November and December, and an elevated number of pregnant females or fertilized embryos in March and July, suggesting that ovulation and fertilization occurred mainly from December to July. In contrast, Coelho et al. (2017), reported a high number of immature (age 0) and juvenile (age 1) individuals in the Southwestern Atlantic, indicating that there is a higher occurrence of smaller-sized specimens at higher latitudes.

Diet

Considered a generalist consumer, *P. glauca* has a diverse diet, with teleost fish and cephalopods (mainly squid) being the groups of highest occurrence reported by

Table 2. Biological parameters for the blue shark, *Prionace glauca*, in the Indian Ocean, North and South Pacific, and North and South Atlantic.

Source	Length range (cm)	Size at maturity (cm)		Length measurement	Fecundity (number of embryos)	Gestation (months)	Size of embryos
		Male	Female				
<i>Pacific Ocean</i>							
Fujinami et al. (2018)	33.4–252.0	160.9	156.6	PCL	1– 112 (33.1 mean)	11	1.2–41.2
Bustamante and Bennett (2013)	52.0–310.0	190.3	199.2	TL	–	–	–
Zhu et al. (2011)	124.0–277.0	–	–		13–68 (35.0 mean)	–	12–39
Francis and Duffy (2005)	50.0–270.0	190–195	170–190	FL	–	–	–
Stevens and McLoughlin (1991)	232.0–300.0	–	–		11–49 (34.0 mean)		2.7–13.2
<i>Atlantic Ocean</i>							
Briones-Mendoza et al. (2016)	130.0–307	187.1	–	TL	–	–	–
Montealegre-Quijano et al. (2014)	80–258	180.2	171.2	FL	9–74 (33.5 mean)	–	18–33
Jolly et al. (2013)	72.0–313.0	201.4	194.4	TL	43–55	–	–
Megalofonou et al. (2009)	70–349	202.9	214.7	TL	–	–	–
Bornatowski and Schwingel (2008)	197–295.5	195.0	185.0	TL	210 (34.2 mean)	–	24–45
Campana et al. (2005)	–	201.0	–	–	–	9–12	40–51
Lessa et al. (2004)	173.8–310	225.0	228.0	TL	–	–	–
Henderson et al. (2001)	64.0–228.0	190.0	–	TL	–	–	–
Castro and Mejuto (1995)	150.0–260.0	225.0	180.00	FL	35.0 (mean)	–	3–35
Hazin et al. (1994)	156.0–228.0	205.0	162.0	FL	30.0	–	2–26
Stevens (1984)	218.0–326.0	216.0	218.0	TL	4– 57 (32.0 mean)	9–12	46–51
Pratt (1979)	93.0–282.0	183.0	180.0	FL	60	9–12	35–44
<i>Indian Ocean</i>							
Varghese et al. (2017)	186.0–280.0	207.1	–	TL	–	–	–

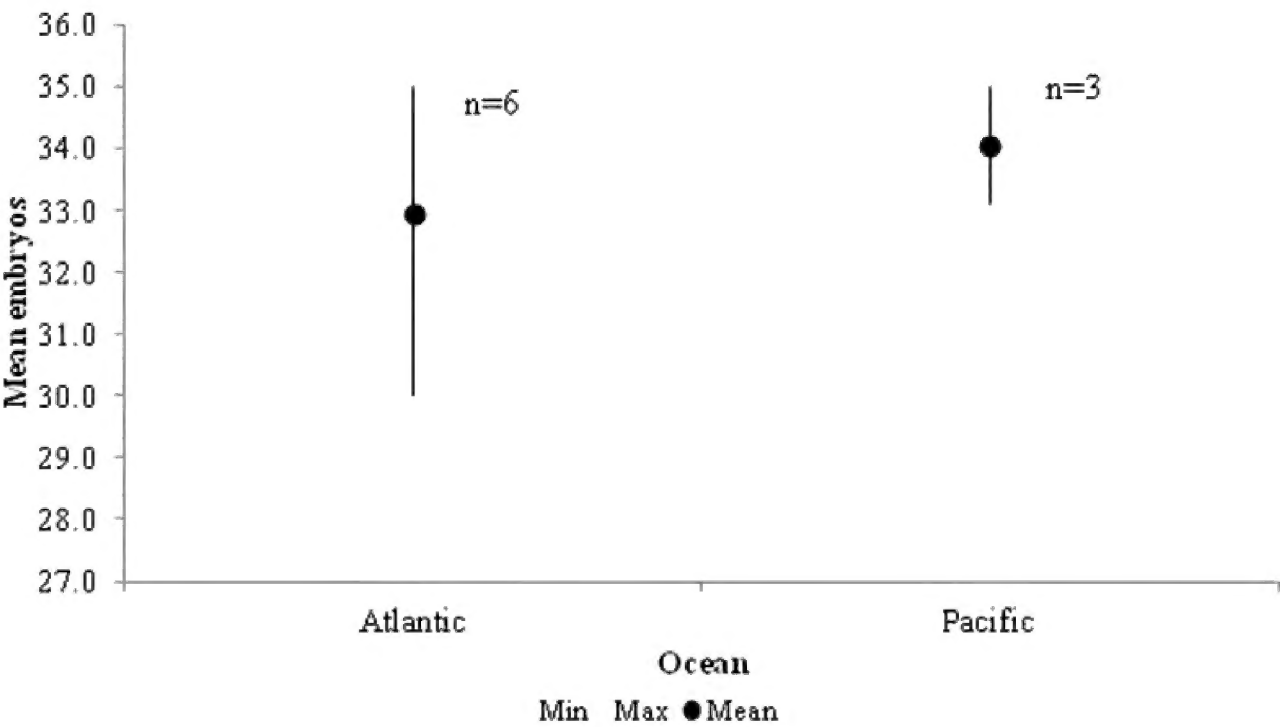


Figure 3. Average (dots), minimum and maximum (bars) of absolute fecundity of *Prionace glauca* in different oceans.

studies on stomach content (Stevens 1984; Henderson et al. 2001; Kubodera et al. 2007; Bornatowski and Schwingel 2008; Markaida and Sosa-Nishizaki 2010; Loor-Andrade et al. 2016; Rosas-Luis et al. 2017). Henderson et al. (2001) reported that a large portion of the fish species found in the digestive tract are epi and mesopelagic,

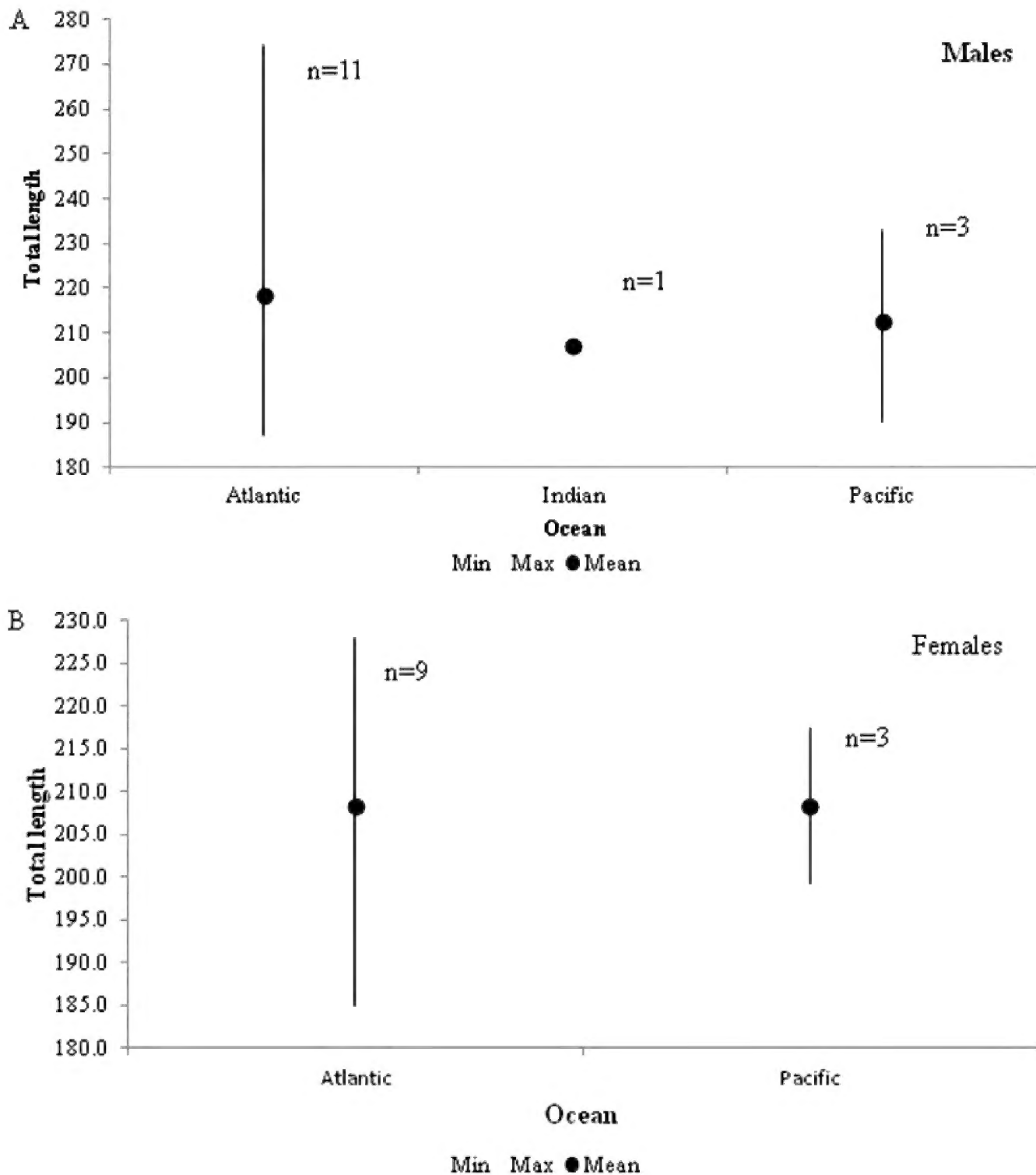


Figure 4. A and B average (dots), minimum and maximum (bars) of maturity (L50) for male and female blue sharks.

thus reinforcing that *P. glauca* feeds mainly on relatively abundant pelagic species. Regarding the consumption of cephalopods, Loo-Andrade et al. (2016), observed that it is seasonal, corroborating McCord and Campana (2003).

Indeed, the blue shark is not a fast swimming predator due to its morphological characteristics, showing preference for slow-moving prey (Vaske et al. 2009). Some studies mention differences in diet between sexes and age classes. McCord and Campana (2003) reported significant differences between sexes during ontogenetic development. Furthermore, feeding habits vary within the Atlantic Ocean, with blue sharks in the South feeding mostly on fish, while the population in the North feeds on fish and cephalopods (Fig. 5).

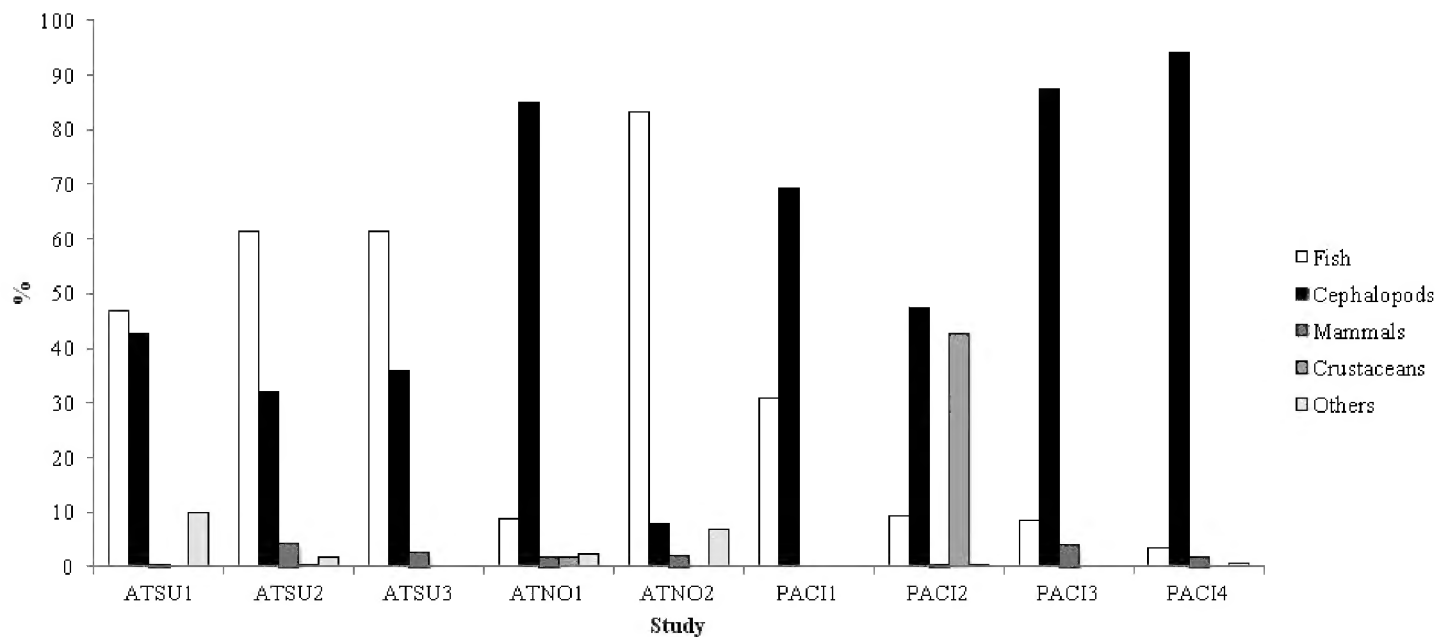


Figure 5. Frequency of prey identified in the stomach content of the blue shark in studies of the South Atlantic (ATSU); North Atlantic (ATNO) and Pacific (PACI) Oceans.

Demography

In the Atlantic Ocean, the blue shark had an intrinsic rate of increase (r) of 0.1882 and a population doubling time of $t_{x2} < 3.8$ years, with the intrinsic rate of 0.355 year^{-1} (Chen and Yuan 2006). Aires-da-Silva and Gallucci (2007) reported that the stock in the North Atlantic is highly productive, with an annual finite rate (λ) of 1.23 year^{-1} and the average time of 3.1 years (t_2), indicating a high growth rate in the absence of capture. In the South Atlantic, different scenarios were created to estimate population growth. Assuming absence of capture and considering a 65.9% survival in the first year of life, the population would grow 24.2% every year. However, based on fishing mortality data, with an initial survival of less than 27.4%, the population would shrink (Montealegre-Quijano and Vooren 2009). According to Chen and Yuan (2006), the intrinsic rate decreases as fishing mortality increases. When r is positive and/or close to zero, the population is growing despite the fishing toll. When r is below zero, populations are decreasing and are likely overexploited.

In the South Atlantic, fishing mortality influences populations, leading to a declining trend due to smaller sizes and maximum age. Estimates of annual natural mortality (0.256 for females and 0.243 for males) correspond to 77.5 and 78.5% of survival, while total mortality (0.601 for females and 0.589 for males) reaches 55% for both sexes. According to Aires-da-Silva and Gallucci (2007), the survival of juvenile sharks is a key factor for blue shark productivity, significantly contributing to population growth and presenting an average elasticity of 57.7% for ages 0–4.

Demographic analyses are deterministic and stochastic methods of stock assessment commonly use *age-based* or *stage-based* life data (Cortés 1998; Mollet and Cailliet 2002; Chen and Yuan 2006; Cortés 2007; Santana et al. 2009), such as sexual maturity, maximum breeding age, and mortality and birth rates (Cortés 1998;

Takeuchi et al. 2005). However, these data are generally not available or insufficient to estimate natural and fishing mortalities (Takeuchi et al. 2005).

This model aims at estimating the productivity of a given population, characterizing its vulnerability to exploitation (Cortés 2007), contributing to the efficient management of shark stocks (Chen and Yuan 2006), being an essential tool to help highly exploited or threatened species due to overfishing (Santana et al. 2009). The estimated parameters of the demographic analysis are R_0 (Reproductive rate), T (Generation time), r (Intrinsic population growth rate) and λ (Finite rate of population growth) (Mollet and Cailliet 2002). Furthermore, the Monte Carlo simulation is employed to integrate uncertainty of demographic parameters (Cortés 2002). Therefore, scenarios on population behavior gleaned from the survival of juveniles and adults, fecundity and fishing, are analyzed and demographic parameters are generated.

According to Tavares et al. (2012), the stock structure and population demography of the blue shark in the Atlantic Ocean are uncertain, with at least three stocks: one in the North Atlantic, one in the South Atlantic, and another one in the Mediterranean Sea. In the South Atlantic, depending on the scenario of initial survival and absence of capture, the reproductive potential would be enough to compensate for natural mortality. In other words, if the age-at-fisheries-recruitment is 7 years, the maximum reproductive potential is reached and the population would have a growth capacity of 10% (Montealegre-Quijano and Vooren 2009). Considering the biological data on this species, for which maturity is reached at around 5 years, a fisheries recruitment at 7 years would decrease the fisheries impact on this species.

Conservation

Despite being a highly-exploited species, the blue shark is classified as Near Threatened both in IUCN's (Stevens 2009) and the Brazilian Red Lists (ICMBio 2016). The global status was evaluated with an estimate of 10.7 million blue sharks being killed every year (Dulvy et al. 2008). Observing the stock assessments, ICCAT played an important role over the years. In 1995, it created the first resolution on the status of stocks and bycatches of shark species and carried out an assessment of the stocks of the blue shark and the shortfin mako shark in 2004. Additionally, ICCAT was responsible for implementing the resolution, which requested all available information on shark fishing until 2004, since a limited number of nations had developed their National Plans of Action for the Conservation and Management of Sharks (NPOAs) (Levesque 2008). These measures have contributed to reducing fishing mortality for oceanic sharks (Camhi et al. 2008).

In the North Atlantic, blue shark populations have the decline estimated at over 60% between 1986 and 2000, with high fishing pressure being the main cause (Baum et al. 2003). This estimate is also repeated in the South Atlantic. According to the cartilaginous fish assessment, about 33% of the species are at some level of threat, with commercial fishing being the main cause. The blue shark is one of the most studied species, especially regarding its distribution, abundance, and biology. Its wide movements,

crossing national and international borders, are one of the obstacles for management and conservation initiatives (Queiroz et al. 2010). Canada, like many other countries, adopted preventive measures to guide the exploitation of pelagic sharks, for which the management plan establishes non-restrictive landing guidelines as a way of safeguarding a biologically sustainable resource and a self-sufficient fishery (Campana et al. 2002).

In Brazil, only Rio Grande do Sul state has specific legislation on which landings are prohibited, through the State Decree 51.797/2014, where some species were declared as threatened with extinction, as for example the blue shark included in the “Vulnerable” category, with a high risk of extinction in the medium term. However, in other regions of Brazil, this species continues to be legally exploited.

Final considerations

Although there are many studies on blue sharks, information is sparse and can lead to errors when dealing with its biological parameters in some locations. Studies show that *P. glauca* is the most widely distributed and fished shark species in the world. Regarding the reported catches of *P. glauca*, the Pacific Ocean has the highest volumes. These works report a concern about the catch levels, suggesting that the available information may not represent what is actually captured, due to illegal fishing and finning, which are generally not recorded.

Widely exploited, the global conservation status of *P. glauca* is near threatened with extinction (NT) (Stevens 2009). Despite this classification, there are no restrictions on the capture of this species in some regions, even though fishing mortality is the main source of impacts.

Once knowledge of stock structure is enhanced, it will be possible to delineate a more adequate assessment. Furthermore, it will be possible to establish more effective conservation measures including no-capture zones or seasonal closures, mandatory release of pregnant and juvenile females, establishing catch quotas, and engaging the fishers and society on the importance of this species’ conservation.

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